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Intransitive competition is common across five major taxonomic groups and is driven by productivity, competitive rank and functional traits

Soliveres, Santiago ; Lehmann, Anika ; Boch, Steffen ; Altermatt, Florian ; Carrara, Francesco ; Crowther, Thomas W ; Delgado-Baquerizo, Manuel ; Kempel, Anne ; Maynard, Daniel S ; Rillig, Matthias C ; Singh, Brajesh K ; Trivedi, Pankaj ; Allan, Eric

Abstract: 1. Competition can be fully hierarchical or intransitive, and this degree of hierarchy is driven by multiple factors, including environmental conditions, the functional traits of the species involved or the topology of competition networks. Studies simultaneously analysing these drivers of competition hierarchy are rare. Additionally, organisms compete either directly or via interference competition for resources or space, within a local neighbourhood or across the habitat. Therefore, the drivers of competition could change accordingly and depend on the taxa studied. 2. We performed the first multi-taxon study on pairwise competition across major taxonomic groups, including experiments with vascular plants, mosses, saprobic fungi, aquatic protists and soil bacteria. We evaluated how general is competition intransitivity from the pairwise competition matrix including all species and also for each possible three-species combination (triplets). We then examined which species were likely to engage in competitive loops and the effects of environmental conditions, competitive rank and functional traits on intransitive competition. 3. We found some degree of competition intransitivity in all taxa studied, with 38% to 5% of triplets being intransitive. Variance in competitive rank between species and more fertile conditions strongly reduced intransitivity, with triplets composed of species differing widely in their competitive ranks much less likely to be intransitive.

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Intransitive competition is common across five major taxonomic groups and is driven by productivity, competitive rank and functional traits.

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Running head: Drivers of intransitive competition

Summary

1. Intransitive competition can be driven by multiple factors, including environmental conditions, the functional traits of the species involved or the topology of competition networks. Studies analyzing simultaneously these drivers are rare and their effects on intransitive competition poorly understood. Additionally, organisms compete either directly or via interference competition for resources or space, within a local neighbourhood or across the habitat. Therefore, the drivers of competition could change accordingly and depend on the taxa studied.

2. We performed the first multi-taxon study on pairwise competition across major taxonomic groups, including experiments with vascular plants, mosses, saprobic fungi, aquatic protists and soil bacteria. We evaluated the degree of intransitivity from the pairwise competition matrix and for each possible three-species combination, and also the effects of environmental conditions, the competitive rank, and functional traits on intransitive competition.

3. Intransitive competition prevailed in all taxa, but was less likely under fertile conditions. A strong predictor of intransitive competition was the variance in competitive ranks of the species involved in each three-species combination (triplets). Triplets formed by species widely differing in their competitive ranks were much less likely to be intransitive than those formed by species with similar competitive ranks.

4. Including functional traits of the species involved more than doubled the variation explained by models including competitive rank only, although the relevant traits were taxon-dependent. Half of this variation was related to the individual traits of the species involved, and the other half to the variability in such traits, which generally reduced the odds of a given species combination being intransitive.

5. *Synthesis*: Our study comprehensively evaluated the drivers of competition across multiple taxa and showed that productivity and competitive rank are fundamental drivers of intransitivity. In one of the first studies to do so, we showed that not only the functional traits of each species, but also those of the accompanying species, determine competition intransitivity. Our study illustrates the generality of intransitive competition while showing its environmental and species-specific drivers, and also highlights how multi-taxon approaches help drawing general patterns in this coexistence mechanism.

Key-words: bacteria, bryophytes, competition hierarchy, coexistence, functional traits, protists, rock-paper-scissors, saprobic fungi, vascular plants.

Introduction

The lack of competition hierarchy (intransitive competition) is the equivalent to the rock-paper-scissors game in that no single species can outcompete all the others, and therefore local extinctions are avoided (Gilpin 1975; Laird & Schamp 2006; Rojas-Echenique & Allesina 2010). Intransitive competition can occur if there are reciprocal competitive advantages. For example, a system could exhibit an intransitive loop if species A competes more effectively for nutrients than species B ($A > B$), B outcompetes C ($B > C$), but C is able to prevent resource uptake, reproduction or growth by species A through interference competition, e.g. the production of allelochemicals ($C > A$; Aarsen 1992; Lankau & Strauss 2007; Gallien 2016). Intransitive competition is gaining attention as a potential mechanism for species coexistence (Laird & Schamp 2006; Allesina & Levine 2011; Soliveres *et al.* 2015; Maynard *et al.* 2017a) and could also be related to other important community and ecosystem attributes such as spatial patterning, sensitivity to exotic invasions or diversity-function relationships (Vandermeer & Yitbarek 2012, Henriksson *et al.* 2016, Maynard, Crowther & Bradford 2017b).

Intransitive competition has been described in many taxa (see reviews in Gallien 2016, Soliveres & Allan, in press). However, given the wide range of ways that different organisms can compete, studies that focus on interactions within single taxonomic groups cannot draw general conclusions about the extent of intransitive competition in nature, or the factors driving it. In general, all taxa within a trophic level and with similar environmental preferences will compete against each other for key resources directly (e.g. nutrient uptake) or indirectly (e.g. allelopathic compounds), although the relative importance of resource or interference competition can vary substantially between organisms.. For example, mosses, intertidal organisms or fungi might compete mostly for space and this competition can be dominated by interference mechanisms, which individuals use to prevent overgrowth by others (Buss 1980; Maynard *et al.* 2017a). Conversely, plants, protozoa or bacteria may

92 compete more directly for resources although sessile organisms do so more locally than
93 mobile organisms. Intransitivity in competition networks may decline in well-mixed
94 communities (Reichenbach, Mobilia & Frey 2007; Laird & Schamp 2015; Yitbarek &
95 Vandermeer 2017) and therefore could be less common for mobile taxa. The lack of studies
96 applying common methodologies across taxonomic groups, together with the different
97 prevailing modes of competition within each taxon, limits our capacity to evaluate the extent
98 of intransitive competition in nature, and to identify generalities in the factors driving it.

99 The degree of intransitivity observed in a community may also depend on
100 environmental conditions such as productivity or heterogeneity (Gilpin 1975; Allesina &
101 Levine 2011; Schreiber & Killingback 2013). However, empirical evidence for these
102 environmental effects remains rare (Dormann 2007; Bowker, Soliveres & Maestre 2010a;
103 Soliveres *et al.* 2015; Ulrich *et al.* in press). Productivity might reduce intransitivity through
104 two different mechanisms: i) if it allows very competitive species to enter the system,
105 imposing stronger competitive hierarchies (e.g., Soliveres *et al.* 2015; DeMalach, Zaady &
106 Kadmon 2017), or ii) if it reduces the number of resources species compete for (e.g., Harpole
107 & Tilman 2007). Heterogeneity, in turn, can increase intransitivity by the opposite
108 mechanisms, reducing competitive hierarchies and allowing the species to compete for a
109 larger variety of resources (Allesina & Levine 2011; Schreiber & Killingback 2013).
110 However, a higher productivity could also increase the pool of competing species or the
111 importance of competition for community assembly, potentially increasing the role of
112 intransitive competition as driver of coexistence (Gilpin 1975; Bowker *et al.* 2010a).

113 In addition to the environment, the functional traits of the species competing are
114 important determinants of the outcome of pairwise competition (Schamp, Chau & Aarsen
115 2007; Kunstler *et al.* 2012; Herben & Goldberg 2014; Kraft, Godoy & Levine 2015).
116 According to the limiting similarity theory, species should differ in their functional traits to
117 avoid competition via niche differences (e.g., Herben & Goldberg 2014), however, similar

traits can equalize fitness differences, also leading to species coexistence (Mayfield & Levine 2010; De Bello *et al.* 2012). In this regard, if intransitive competition is fostered by reciprocal competition, then we would expect differentiation across resource-acquisition strategies (i.e., trait differences) to enhance intransitivity. However, very heterogeneous competitive abilities (i.e., trait differences) can also hinder the effect of intransitive competition on coexistence (Gallien *et al.* 2017), and thus trait differences could also reduce intransitivity. Functional traits could therefore alter the degree of intransitivity in competition networks, although this effect is poorly understood (Gallien 2016; Maynard *et al.* 2017a). It has also been hypothesized that intransitive competition networks are nested, meaning that the dominant species form intransitive loops but that hierarchical competition occurs between dominant and subdominant species (Soliveres *et al.* 2015). Thus, the competitive ranks of the species, or their functional traits (if these are linked to competitiveness), could affect the likelihood that species form an intransitive loop (see also Laird & Schamp in press). Despite the prominent role that functional traits could have in determining intransitivity in competition networks; their effect as drivers of competition intransitivity and their interplay with environmental drivers or focal taxa is still poorly understood.

Here we explore the generality of intransitive competition in nature by combining re-analyses of published (Carrara *et al.* 2015a; 2015b; Delgado-Baquerizo *et al.* 2017; Maynard *et al.* 2017a) and new pairwise competition experiments to explore the generality and nestedness of intransitive competition in nature. These include 124 species across five different taxonomic groups: vascular plants, mosses, saprobic fungi, soil bacteria and aquatic protists. For mosses and bacteria, we also analyzed how increasing productivity affected the degree of intransitivity in the competition network. Finally, we examined the effect of the functional traits of competing species as drivers of intransitive competition. Our hypotheses were: i) intransitive competition is widespread across the taxa studied, but less pronounced in mobile taxa such as protists and bacteria, ii) intransitive competition is reduced (competition

is more hierarchical) in more productive environments, iii) intransitive competition networks prevail between dominant species, but not between them and the rest of species (i.e., they are nested), iv) the functional traits of the competing species influence the degree of intransitivity in their competition, and v) the functional traits driving intransitive competition change under contrasting environmental conditions and with the focal taxa.

Materials and methods

PAIRWISE COMPETITION EXPERIMENTS

Experimental designs and species numbers differed depending on the taxa studied; however, all possible inter-specific pairwise combinations and monocultures were realized for all taxa.

Vascular plants: seeds of 20 species (see species identities in Suppl. Table S1) were bought from a commercial supplier (UFA Samen, Switzerland) and the seedlings were grown in every possible pairwise combination for seven months (one replicate per combination). This was done in 2 L pots filled with a mix of commercial soil (Ricoter, Aarberg, Switzerland) and sand. After the seven months, the aboveground biomass was harvested for each species at each pot.

Mosses: biomass samples from 10 different species growing in grasslands of southwestern Germany were taken. Then, air-dried moss material (3 mg of each species) was used to start the competition experiments. All pairs of species were replicated three times and were grown in 5 cm Petri dishes filled with commercial peat-based seedling substrate (Klasmann-Deilmann GmbH, Germany; 80% peat, 20% coconut fibers; N 90mg/l, P2O5 100mg/l; K2O 250 mg/l, buffered with CaCO₃ to pH 5.5). The Petri dishes were watered every second day until one month after mosses covered all the space in more than half of the Petri dishes (7 months in total). After this period, the cover of each moss species was estimated as a measure of its abundance.

Saprobic fungi (EU): all pairwise combinations between thirty-one species of saprobic fungi from Central Europe (hereafter EU fungi) were grown on potato dextrose agar in 9 cm Petri dishes. To inoculate the fungi, previously sterilized and subsequently colonized poppy seeds (two poppy seeds per plate) were used. After four weeks of growth at 22°C, the outcomes of each pairwise competition were scored as draw (if no species overgrew the other or if mutual intermingling without growth inhibition occurred), a win (if the target species overgrew its enemy) or a loss (if the target species was overgrown).

Saprobic fungi (US): thirty-seven isolates from wood decay Basidiomycete fungi from North American populations (hereafter US fungi) were grown in 10 cm Petri dishes filled with 2% (w/v) malt extract agar. For each pairwise competition experiment, two competing species were inoculated using three plugs placed at equal distances (see details in Maynard *et al.* 2017a). After eight weeks at 22 °C, competition was inferred from whether one species overgrew the other or not.

Protists: every possible pairwise combination of a set of 10 protists and one rotifer species (hereafter “protists” for simplicity) were grown in microcosms with 10 mL sterilized culture medium and 0.45 g · L⁻¹ of protozoan pellets (Carolina Biological Supply, NC USA; 6 replicates per combination; see Altermatt *et al.*, 2015; Carrara *et al.* 2015a; Carrara *et al.* 2015b for further details). After 21 days at constant environmental conditions, the density for each protist species within each pairwise combination and monoculture was recorded to infer the outcome of competition.

Bacteria: strains from six terrestrial dominant bacterial taxa were isolated from natural soil (see Delgado-Baquerizo *et al.* 2017 for details). Bacterial cultures were inoculated at equal abundances in 10 g of two different soils (gamma-sterilized) and were grown in hermetic containers for 8 weeks. Every pairwise combination was realized between these six bacterial cultures once, accounting for a total of 15 microcosms. After 8 weeks, the relative abundance (number of gene copies · g⁻¹ soil) of each bacterial strain was quantified using qPCR.

MEASURING INTRANSITIVITY

In all cases, individuals of each species were either grown with a neighbor of their own (intra-specific competition) or another (inter-specific competition) species. This allows a comparison of the relative performance of each species after accounting for differences in intrinsic growth rates by using the relative yield of each species (Keddy & Shipley 1989; Grace *et al.* 1993; Dormann 2007): $RY_i = \text{performance of species } i \text{ growing with species } j / \text{performance of species } i \text{ growing in monoculture}$. Our performance measures were aboveground biomass (vascular plants), percentage cover (fungi, mosses) or abundance (number of cells for protists, number of gene copies for bacteria) of each target species in each possible pairwise combination, which generated a species by species competition coefficient matrix. In the US saprobic fungi, intra-specific competition could not be calculated, so competition was inferred from the overgrowth data. For those pairwise competition experiments in which we had replicates (mosses, protists and bacteria), the average across those replicates was used to calculate relative yields. The competition coefficients within the matrix were transformed to a binomial variable to obtain a single “winner” in each pairwise competition (1 if $RY_i > RY_j$; 0 otherwise; where i and j are the species in the row and the column of the matrix, respectively; see Suppl. Material S2 for a worked example). Draws were considered as 0 for both sides of the matrix (i against j , and j against i), so it did not influence our measure of (in)transitivity. The transformation of RYs into a binomial variable allow calculating the level of intransitivity as the number of competitive reversals (i.e., 1s below the upper diagonal once the matrix has been re-ordered to have the maximum number of wins in the upper diagonal; Suppl. Material S2; Laird & Schamp 2006; Ulrich *et al.* 2014).

After ordering the terms within the matrix by row and column totals, such as the competitive dominant species (the one with more wins) remains up and to the right within the matrix (see worked example in Suppl. Material S2), the degree of intransitivity was calculated

for each group as the number of competition reversals ($RY_i < RY_j$) which occurred (Ulrich *et al.* 2014; modified after Petraitis 1979; Laird & Schamp 2006). This metric counts the number of competitive reversals, i.e. where the species in the column (j) displaces the species in the row (i). The number of reversals is likely to increase as more species (m) are considered (e.g., Grace, Guntenspegen & Keough 1993). Thus, our metric is the normalized number of competition reversals after accounting for all potential pairwise combinations, so that: $I = (2 \cdot (RY_i < RY_j)) / (m \cdot (m-1))$, where zero/one values indicate completely transitive/intransitive communities. It must be noted that converting RYs to 1s and 0s may potentially overestimate the extent of intransitive competition by assuming as competitive reversals random competitive reversals between species with similar competitive strengths. And this limitation is particularly important when pairwise competition experiments are conducted without replication (such as in our vascular plants and fungi). To address this issue, we calculated a new metric (*Inest*) based on the “nestedness” of the matrix, which allows using all the information from the RYs (see Fig. S2b in Ulrich *et al.*, in press). By using directly the RYs, we minimize the influence of very similar competitive reversals (e.g., $RY_j = 0.53 > RY_i = 0.47$, in comparison with $RY_j = 0.90 > RY_i = 0.10$) in our estimation of intransitivity. This metric also requires re-ordering the species \times species competition matrix by row and column sums to maximize the “wins” in the upper diagonal, but not transforming the RYs to 0s and 1s. Instead, *Inest* calculates the difference between the RYs in the upper diagonal vs those below (e.g., RY_{AB} vs RY_{BA} in the worked example in Suppl. Material S2, see also Ulrich *et al.*, in press), weighting those differences by the distance of the position of a particular RY to the diagonal of the matrix. Both metrics of intransitivity (I and *Inest*) rendered very similar results (Suppl. Material S3), and therefore we only present here those of I as they are more straightforward to understand and more conservative in our case.

It has been argued that relative yields are not a good proxy of long-term competitive outcomes or fitness differences between two competing species (Levine *et al.* 2017).

However, this important limitation seems to be constrained to cases in which the intra-specific competition coefficient of one species in a pair is four or more times bigger than the other, which seems unlikely in nature (see full rationale and results in Suppl. Material S4). Relative yields on biomass (or related measures) were used here in order to get comparable metrics for all of our taxa. However, it must be noted that, as with other metrics of biotic interactions (e.g., Holmgren, Scheffer & Huston 1997), results can strongly depend on the performance measure used and could be different if using survival, number of seeds or total extinctions as a measure of competition displacement (see e.g., Carrara *et al.* 2015a, 2015b).

Single measures of competition intransitivity may fail to fully account for the drivers or consequences of these competitive networks (Laird & Schamp 2009; Alcántara, Pulgar & Rey 2017). Therefore, to complement the community-level *I* metric, additional metrics based on three-species combinations (hereafter triplet) were calculated. To do so, the existence of competitive reversals ($A < B < C < A$; rather than $A < B < C$ and $A < C$) was evaluated for each possible triplet within the species pool, so there were two possibilities: i) the triplet does not have competitive reversals, and therefore is fully hierarchical, and ii) the triplet has a competitive reversal and therefore is intransitive. To calculate whether a triplet is intransitive or not, we performed a 3-species version of the first method: i) convert RY to 1 and 0s, ii) order matrix by row and column totals, and iii) if after re-ordering all the 1s are in the upper diagonal, then the triplet is transitive, if not, then it is intransitive. Considering intransitivity in each triplet allowed us to investigate the effects of the environment (i.e., productivity), the mean characteristics of the species (i.e., competitive rank, functional traits) and the variation in species characteristics (variance in competitive rank and functional traits) on intransitivity.

DRIVERS OF INTRANSITIVITY

-Competitive rank

Intransitive competition has been hypothesized to be nested, i.e., prevail within guilds of competitively dominant or subordinate species, but not between these guilds (Soliveres *et al.* 2015), although this hypothesis has not been tested experimentally. The nestedness of intransitive competition networks was evaluated by measuring how competitive rank (using the average competitive rank across three species in a given triplet) affected the probability of such triplet to participate in an intransitive loop. Competitive ranks were directly obtained from the pairwise competition matrix once ordered by row and column totals. After ordering, the species above are the strongest competitors (the ones with more wins) whereas the species below are the weaker competitors. Therefore, the row number occupied by each species in the pairwise competition matrix informs us about its competitive rank (the smaller the row number, the stronger the competitor). According to the nestedness hypothesis, species largely differing in their competitive ranks should not form intransitive loops. Thus, we expected a negative effect of the variability in competitive ranks covered by the three species forming a triplet on the probability of this triplet to be intransitive. The variability was measured as the Rao's Q of competitive rank across the three species.

-Functional traits

Functional traits are related to competitive ability, but also can offer additional information on how species differentiate in the ways they compete (e.g., reciprocal competitive advantages) and on how they respond to environmental changes. Thus, in addition to the effects of competitive rank, the effects of functional traits related to growth rate, environmental tolerances or resource use on intransitive competition were also considered. The average of each trait across the three species in a triplet was considered to test if particular types of

species are more likely to participate in intransitive loops, and the Rao's Q of each trait was used to assess if intransitivity is more or less common between functionally different species.

Relative growth rate was available for all taxa as the rate of biomass (or cover) accumulation over a given period of time for isolated, not competing, individuals. Since for all the species we started with exactly the same biomass (or cover), a single data point suffices to calculate relative growth rate. Since this is likely to be an important trait related to competitive ability, it was included as a common predictor for all taxa. For vascular plants, plant height, specific leaf area, seed mass, leaf dry matter content and leaf N content (obtained from the TRY database; Kattge *et al.* 2011) were also included. These traits are linked to resource-use strategy and competitive ability in plants (Schamp *et al.* 2007; Herben & Goldberg 2014; Reich 2014). For mosses, colony type (three types depending on the degree of compaction: rough mat, smooth mat and weft; from maximum to minimum colony compaction) and mean shoot length (obtained from the Bryoatt database; Hill *et al.* 2007) were included in the analysis. Empirical links between moss functional traits and competition are scarce, although based on results for vascular plants and theory (Cornelissen *et al.* 2007), these traits should be important drivers of competition between mosses (Bowker, Maestre & Escolar 2010b). For the US fungi, traits related to chemical aggressiveness (hydrolytic enzymatic activities), ability to overgrow other colonies (growth rate and density of the colony) and nutrient uptake (wood decomposition, enzymes related to C and P cycling) were obtained for published literature (Maynard *et al.* 2017a; see details in Suppl. Table S1). For soil bacteria, growth rate (i.e., abundance) in monoculture and enzymes related to their ability to capture P and degrade different sources of C were considered (data from Delgado-Baquerizo *et al.* 2017). Functional traits for EU fungi were growth rate and phylum. For protists, invasibility (as estimated by Mächler & Altermatt 2012) and functional group (small protists, large protists, mixotrophs; Carrara *et al.* 2015a) were available. These traits are related to feeding guild, environmental tolerances and growth rates.

-Environmental conditions

The role of environmental conditions was evaluated in two of the taxa (mosses and soil bacteria). For mosses, a N-fertilization treatment was added to our pairwise competition experiment, aiming to increase productivity and therefore affect the degree of intransitivity (Gilpin 1975; Bowker *et al.* 2010a). Similarly, soil bacteria were cultivated in two soils differing in their organic matter content and pH, which strongly affects the abundance of soil bacteria (e.g., Lauber *et al.* 2009; Maestre *et al.* 2015) and can also be seen as representing different levels of productivity. Our experimental results were compared with observational data from mosses growing in areas that differed in productivity (Suppl. Material S5).

STATISTICAL ANALYSES

-How widespread is intransitive competition?

First, our six *I* metrics (one per group, with EU and US fungi analyzed separately as they followed slightly different approaches) were compared with 0 (values of $I = 0$ are related to perfect competition hierarchy as no competitive reversals are observed in the community) using a t-test. To examine the role of mobility in affecting the degree of intransitivity, the difference in *I* between mobile (protists and bacteria) and sessile (vascular plants, mosses and fungi) taxa was analyzed by means of a t-test. In addition, mobility was included as predictor of intransitivity in the triplets together with taxa (added as random factor) using generalized linear mixed models.

-Are intransitive competition networks nested?

The average and Rao's *Q* in the competitive ranks of the three species forming a triplet were considered as predictors of the probability of such triplet to be intransitive. To do this, generalized linear models with the logit link function were performed for each taxon

separately. In the case of bacteria, only one triplet was intransitive, and thus only one predictor could be evaluated each time. Results obtained from these analyses (and also the ones including functional traits, see below) were similar to those using the probability of each species to participate in an intransitive loop (also known as "triangle transitivity"; Shizuka & McDonald 2012). Therefore, only the former are presented as they allow us to compare the effects of the averages vs. the variance of competitive rank and functional traits as drivers of intransitive competition.

-Functional traits as drivers of intransitive competition:

We were interested in comparing the effect of individual traits and the variability covered in such traits by the competing species. Thus, the averages and Rao's Q of the functional traits were analyzed as predictors of the probability of a given triplet to be intransitive (using generalized linear models with the logit link function). All traits and their coefficients of variance were included in our models, together with the average and Rao's Q of competitive rank, for every taxa. In summary, we evaluated sequentially four sets of models:

- i) Intransitivity of each triplet (binomial variable) as response of competitive rank,
- ii) Intransitivity of each triplet (binomial variable) as response of average and variance (Rao's Q) of competitive rank,
- iii) Intransitivity of each triplet as response of competitive rank and average trait values across the three species, and
- iv) Intransitivity of each triplet as response of competitive rank, average trait values across the three species and Rao's Q for competitive rank and functional traits

We evaluated overall model fit by calculating Nagelkerke's pseudo- R^2 as implemented in the function "RsqGLM" of the modEvA package in R. This allowed us to assess the extra variation explained by the functional traits after considering competitive rank. For bacteria, the low number of possible triplets and the low variance in the intransitivity levels of the

triplets (only one was intransitive) prevented us to include more than one predictor each time. Thus, we evaluated each predictor separately, selecting the best (according to their pseudo- R^2 , see below) amongst the averages and amongst the coefficients of variance.

To test whether different traits drive intransitivity in productive environments, the changes in intransitivity in the triplets for moss species competing under the fertile vs control conditions were analyzed using generalized linear models with a logit link function. In these models, fertilization and its interactions with competitive rank and with the functional traits were evaluated. Since no bacterial species were engaged in intransitive competition under fertile conditions, only the data on moss species could be analyzed. In all cases, the triplets within a species pool are not totally independent, as they may share one or two species (e.g., ABC, ABD). To remove this pseudo-replication effect the p-values associated to each predictor in all the models explained above were re-calculated using 1000 permutations as implemented in the “PermTest” function of the pgirmess package in R. All analyses were performed using R version 3.0.2 (R Development Core Team 2013).

Results

HOW WIDESPREAD IS INTRANSITIVE COMPETITION?

All taxa studied, except the soil bacteria growing in rich soils, showed some degree of intransitivity (Fig. 1). Our overall I metric, based on the proportion of the competitive reversals in the pairwise competition matrix, was significantly higher than 0 (pure hierarchical competition): $t = 3.74$, $df = 5$, $P = 0.013$. Importantly, there was substantial variation in the levels of intransitivity found across taxa, with very low values in fungi (US) and bacteria, and much higher levels detected for mosses, vascular plants and protists (Fig. 1). In general, high productivity reduced the degree of intransitivity in the communities, with declines detected in both mosses and bacteria when growing under more fertile conditions, consistent with field observations (Suppl. Material S5). These declines were consistent in both the community-

level I metric (bacteria and mosses; Fig. 1) and in the analyses focusing on the triplets (fertilization effect in the glm for mosses: -5.91 ± 1.90 ; $P < 0.005$). We found no differences between sessile and mobile organisms neither at the community-level ($t = 0.29$, $df = 4$, $P = 0.78$) nor in the triplets (mobility effect in glmm: -0.52 ± 0.78 ; $P = 0.5$). The proportion of intransitive triplets out of the total number of possible 3-species combinations ranged between 38.1% (mosses) to 0% (bacteria in fertile soils; Fig. 1), with higher proportions observed for mosses, vascular plants (18.8%) and protists (16.4%), consistently with the results found for the entire communities. These proportions are similar to those previously reported for annual vascular plants (15-19% in Godoy *et al.* 2017; 17-39% in Matias *et al.*, in press).

ARE INTRANSITIVE COMPETITION NETWORKS NESTED?

We only found support for the hypothesized prevalence of intransitive competition between the dominant species in the fungi (Fig. 2), whereas intransitivity was more common for competitively weak species (higher ranks) in mosses and was not affected by competitive rank in the rest of the taxa studied. However, we found strong evidence of nestedness in intransitive competition networks, with intransitivity being more frequent between species with similar competitive ranks. The coefficient of variance in competitive rank had a strong negative effect on competition intransitivity in vascular plants, fungi and protists, with a similar (non-significant) trend found in mosses and bacteria (Fig. 2).

DRIVERS OF INTRANSITIVE COMPETITION

Competitive ranks (average and Rao's Q) explained, on average, 12% of the variation in the probability of a triplet to be intransitive. This variation rose to 28% when including functional traits. The increasing explanatory power when including functional traits was due to both the average and the variance (Rao's Q) in the functional traits of the competing species (Fig. 3, see also Suppl. Material S6). Although with many inconsistencies across taxa, species

showing traits related to competitive ability were less likely to be involved in intransitive competition, these were tall and high leaf N vascular plants, or fungi that grew faster (EU) or consumed more C (US; Fig. 3, Suppl. Material S6). While variance in competitive ranks consistently decreased the probability of a given triple to be intransitive, trait differences did not have consistent effects. Triplets with high trait variance within them tended to be less intransitive in vascular plants and protists, but not in fungi, mosses and bacteria (Fig. 3, dashed columns).

Despite the strong effect of high productivity on intransitive competition, productivity levels did not change which or how functional traits affected intransitivity in mosses, where this could be tested (no significant traits \times fertilization interactions were found). However, fertilization did influence how competitive rank affected intransitivity in mosses, with the relationship between moss average competitive rank and intransitivity shifting from negative in the control to positive in the fertilization treatment (fertilization \times average competitive rank: 0.91 ± 0.35 ; $P < 0.05$).

Discussion

INTRANSITIVE COMPETITION IS WIDESPREAD ACROSS DIFFERENT TAXA

Our results suggest that non-hierarchical competition is the norm, not the exception, in ecological communities. We found evidence of non-hierarchical competition in all taxa studied, adding to the increasing evidence of intransitive competition between vascular plants (Lankau & Strauss 2007), marine intertidal organisms (Buss 1980), biological soil crusts (Bowker *et al.* 2010a), plankton (Huisman & Weissing 1999), bacteria (Kerr *et al.* 2002) or vertebrates (Synervo & Lively 1996). The apparent prevalence of intransitive competition, across above- and belowground, terrestrial and aquatic communities, suggests that a

presumption of hierarchical competition in most current theories (e.g., Tilman 1982; Chesson 2000) may need to be revised.

Our results contrast with other studies that have found fully hierarchical competition (e.g., Grace *et al.* 1993 in vascular plants; Henriksson *et al.* 2016 in fishes; Friedman, Higgins & Gore 2017 in bacteria). Further, in many other organisms (e.g., insects, birds, mammals) where competition experiments are challenging, the possibility of intransitive competition has hardly been considered. The variety of methods used to measure competition may contribute to this lack of consensus. We used relative yields calculated from species abundances to determine competitive outcomes. Relative yields could reflect reciprocal competitive advantages and affect relative abundances of species and the functioning of communities (e.g., Maynard *et al.* 2017b), but caution should be taken in linking them to long-term processes. Other methods for assessing competitive outcomes, based on long-term survival have shown lower levels of intransitivity in competition networks (e.g., Carrara *et al.* 2015a, 2015b for protists or Godoy *et al.* 2016 for vascular plants; but see Huismann & Weissing 1999; Kerr *et al.* 2002). In addition, whereas some experiments are performed under natural conditions, others keep environmental conditions constant, substantially altering heterogeneity, niche differences and intransitive competition. In general, the choice of the performance measure and the experimental approach can have important implications on how we perceive competition. Such issues are known in other areas where, for instance, dryland plants can compete during the growth phase but still facilitate each other's survival (Holmgren *et al.* 1997). This lack of agreement, and the knowledge gaps existing for some taxa, emphasizes the need to better understand the conditions under which competition is intransitive, how intransitive competition might appear at different life history stages and how this impacts coexistence of species but also their abundances and functioning. Multi-taxon studies following a consistent methodology to evaluate competition, such as the one presented here, are a first step towards addressing this important research gap.

INTRANSITIVE COMPETITION IS DRIVEN BY SPECIES WITH SIMILAR COMPETITIVE RANKS

We found that intransitive loops are more likely to occur between species similar in competitive rank, which suggest that intransitive competition networks are nested (Soliveres *et al.* 2015). This was true for protists, EU fungi and vascular plants, for which a higher variability in the competitive rank of the species participating in a triplet negatively affected the odds of such triplet to be intransitive. The mean rank of species in the triplet had positive, neutral or negative effects on intransitivity depending on the group, meaning that intransitive competition could prevail either between only dominant or only subordinate species, depending on the taxonomic group in question. We hypothesize that intransitivity in general is likely to be caused by trade-offs in competitive ability for different resources, or in resource vs. interference competition, (e.g., C uptake vs aggressiveness; see also Maynard *et al.* 2017b). Assuming that functional traits were not only related to competitive ranks (Suppl. Material S6), but also to the different ways by which different species compete for resources (Kunstler *et al.* 2012; Kraft *et al.* 2015, see also Ulrich *et al.* in press, Saiz *et al.* in press), this could explain the positive effects of trait variation in the intransitivity level of triplets of fungi, mosses or bacteria (Fig. 3) even when the variance in competitive ranks had a negative effect. However, when competing species are too different in their ranks (i.e. between dominant and subdominant species), such reciprocal competitive advantages would not be sufficient to reverse very large competitive ability differences. Recent theoretical work has shown that where competitive ability differences are heterogeneous between pairs of species (e.g. species A and B are much better competitors than C but C is only slightly better competitor than A) the positive effects of intransitive competition on coexistence are reduced (Gallien *et al.* 2017). As it may be unlikely that very large pairwise competitive ability

differences form intransitive loops, it may be more common for intransitive competitive reversals to stabilize coexistence between species similar in competitive ability.

INTRANSITIVE COMPETITION IS DRIVEN BY THE ENVIRONMENT, THE WAY SPECIES COMPETE AND THE FUNCTIONAL TRAITS OF THE TARGET AND COMPETING SPECIES

The conditions under which competition is more likely to be intransitive have only been explored in a handful of mathematical models (e.g., Allesina & Levine 2011; Schreiber & Killingback 2013), and in empirical studies focusing on a single taxon (e.g., Bowker *et al.* 2010a; Soliveres *et al.* 2015; Maynard *et al.* 2017a). However, to our knowledge, no studies have studied simultaneously these different drivers of competition intransitivity and how they change according to the way different organisms compete.

We found that environmental conditions influenced the degree of intransitivity. Specifically, increased productivity reduced the number of competitive reversals in mosses and bacteria, which is consistent with results from field observations in vascular plants and mosses (Soliveres *et al.* 2015; Suppl. Material S5). More fertile and productive conditions could reduce the opportunities for intransitivity through reciprocal competitive advantages by two different mechanisms: i) reducing the number of resources species compete for (Harpole & Tilman 2007), and therefore the potential of trade-offs in competitive ability, or ii) shifting the identity of the resources species are mainly competing for towards those where competition is strongly hierarchical (e.g., from soil nutrients to light; DeMalach *et al.* 2017). In this regard, our study shows that intransitive competition can shift from the dominant to the weak competitors under such productive scenarios (fertilized vs control mosses). This could be explained if dominant species start competing mainly for a single resource whereas the remaining species need to fight for the leftovers using a variety of competition strategies. The relationship between fertility and intransitive competition does not seem, however, to be

monotonic. Field observations (Bowker *et al.* 2010a) and theory (Gilpin 1975) suggest that an increase from very low to moderate productivity levels may enhance intransitive competition by increasing the species pool able to colonize a given site and the number of resources for which species compete, both factors increasing the chance that some species engage in intransitive competition. To identify under which fertility levels intransitive competition is maximized, and whether or not different taxa respond in the same way, is an exciting venue for future research.

Three-species experiments (Kerr *et al.* 2002) and mathematical models (Reichenbach *et al.* 2007; Laird & Schamp 2015; Yitbarek & Vandermeer 2017) suggest that intransitive competition is less frequent in those mobile taxa that compete in “global” neighbourhoods as opposed to those that compete locally (sessile organisms). This is supported by the lack of intransitive competition found in other manipulative experiments with organisms growing in well-mixed environments, such as bacteria (Friedman *et al.* 2017), aquatic protists (Vandermeer 1969), or necrophagous insects (Ulrich *et al.* 2014). Despite this evidence, we found no strong evidence for less intransitivity in mobile taxa, mainly due to the high level observed in protists (but see Carrara *et al.* 2015a) and the moderate levels found in fungi. Mobility can, in theory, allow species to take up resources at different points in space, homogenizing resource distributions and preventing trade-offs in competitive ability for different resources. It might also allow competitive species to avoid the influence of allelopathic compounds, reducing the benefit-cost ratio of producing such toxins (Reichenbach *et al.* 2007). In addition, mobility can allow species to escape competition in well-mixed environments (Fronhofer *et al.* 2015) and lead to greater opportunities for niche differentiation. All these mechanisms could reduce the opportunity for intransitive competition to stabilise coexistence although we found little evidence to support this. Another explanation for the taxon-dependent changes in intransitivity we found is the relative size of the organism vs the habitat in which it was grown. Soil bacteria were grown in a larger

555 medium (relative to their size), and thus could more easily have avoided competition,
556 explaining the low prevalence of intransitive competition in these communities. This is also
557 supported by the lower levels of intransitivity found for US vs EU fungi, as the latter were
558 grown in slightly smaller medium (9 vs 10 cm). Definitely, the taxa-dependent mechanisms
559 that may foster transitive or intransitive competition deserve further attention. Exploring
560 further the effect of mobility, local vs global competition mechanisms and the spatial scales at
561 which intransitivity emerges would allow a better understanding of its effects on coexistence.
562 Apart from mobility, size or competitive rank, we found some evidence that species with
563 traits more related to competitive ability in productive environments were less likely to
564 engage in intransitive competition. This parallels what we discussed above regarding
565 productivity and reciprocal fitness differences and suggests that species adapted to high
566 productivity environments may also be less likely to form intransitive loops. In addition, our
567 study helps linking functional traits, competitive ranks and the role of intransitive competition
568 not only on species coexistence but also on realized functional trait patterns. Previous studies
569 have shown an increase in functional trait diversity under intransitive competition (Maynard
570 *et al.* 2017a, Ulrich *et al.*, in press), but these changes are not always expected (Gallien 2016).
571 Our results suggest that, if intransitive competition is driven by reciprocal competitive
572 advantages (as seems to be the cases for fungi, mosses and bacteria), then it should strongly
573 relate to functionally diverse communities. However, in communities with strong fitness
574 differences, or driven by other mechanisms of competition, large trait differences could relate
575 to large fitness differences (e.g., Mayfield & Levine 2010, De Bello *et al.* 2012, Kraft *et al.*
576 2015) which, taken together with our results, suggest in turn that high intransitivity will relate
577 to low trait diversity. In sum, the relationship between intransitive competition and functional
578 trait patterns seems to depend on the importance of reciprocal competition vs. fitness
579 differences as drivers of coexistence.

It must also be noted that the functional traits driving intransitivity were highly taxon-dependent. Of course, this could be caused by the fact that we included different trait sets for each taxon, according to data availability. However, even where we could use similar traits across taxa, as in vascular plants, mosses and US fungi, the identity of the traits driving competition intransitivity differed substantially. Similarly, the single trait that we had for all our species (growth rate) had different effects depending on the organism. This lack of common trait effects should be considered when applying trait-based approaches to find general patterns across different groups of organism.

CONCLUSION

Using a multi-taxon experiment we found that fertility and competitive rank are generally good predictors of intransitive competition. Intransitivity is common in less productive environments, and between species that are similar in their competitive rank. We also showed the need to be cautious when drawing general conclusions about competition and coexistence from studies on single taxa. Finally, our results illustrate that not only the traits of the target species alone, but the structure of trait values of all competing species is an important driver of competition intransitivity. Our findings help achieving a more predictive understanding of which organisms and species may depend more on intransitive competition for their coexistence, and also provide the first steps towards a more comprehensive theory on the linkage between the role of the topology of competitor networks and diversity patterns in real communities.

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Data accessibility

The data used in this article is available as Appendix S1.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

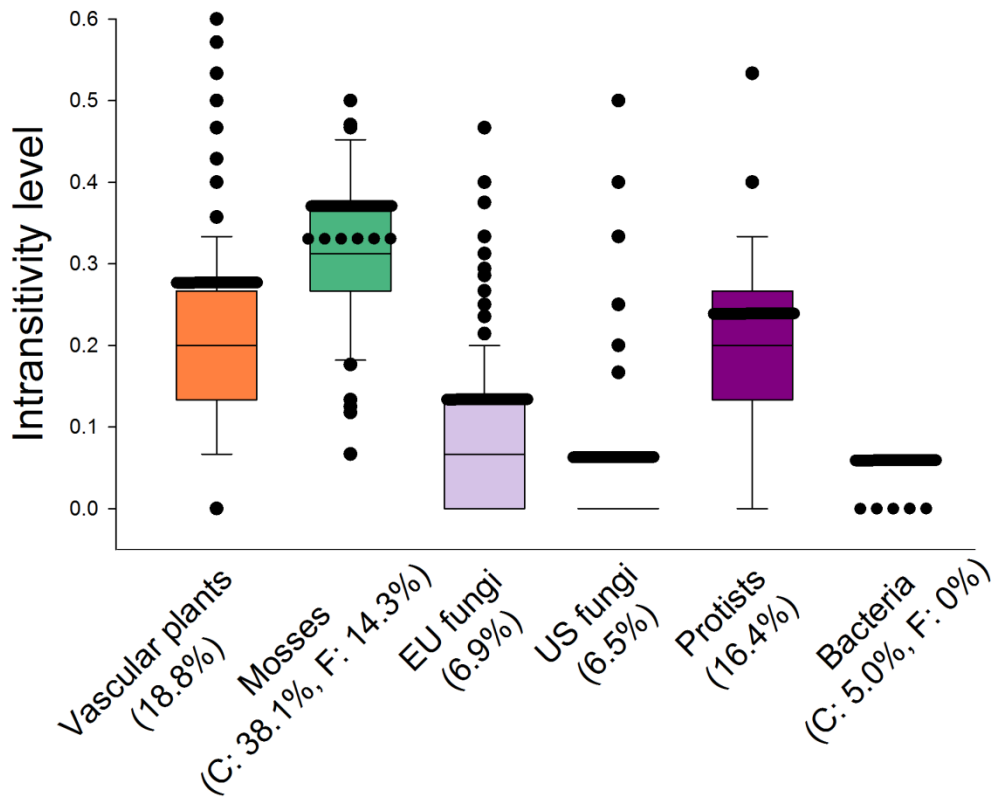


Figure 1. Intransitivity levels across the taxa studied. Thick black dashes show the intransitivity level as calculated using the pairwise experimental approach with all the species. Dotted lines indicate the fertilizer treatment and the fertile soil for mosses and bacteria, respectively. To allow comparison between taxa, the intransitivity level of all possible combinations of 6 species (the minimum species number in the experiments) are shown (box-plots) for all the taxa but soil bacteria. The percentage of all possible 3-species combinations that were intransitive for each taxa are given between brackets (C = control, F = fertile conditions).

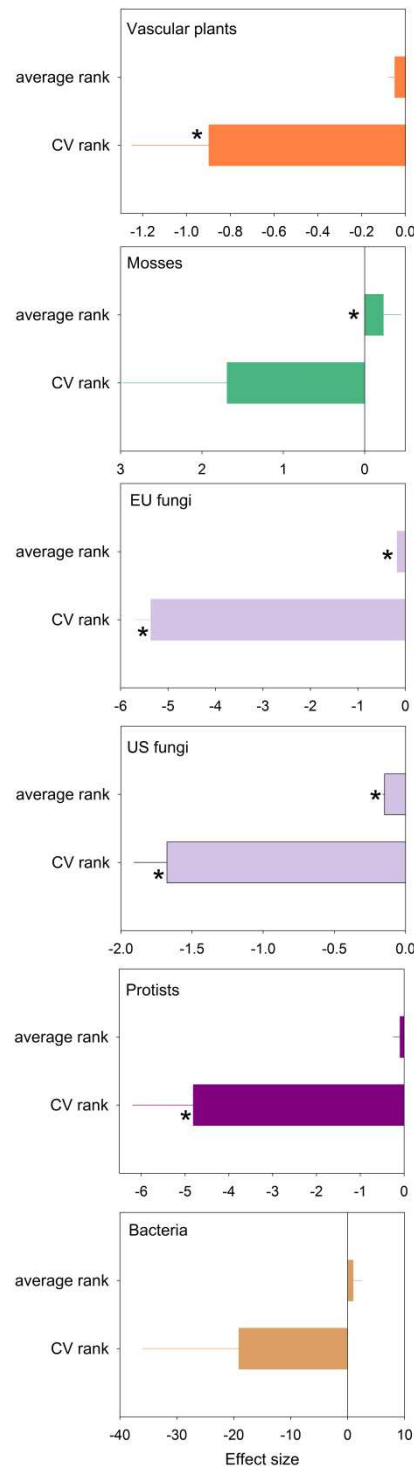


Figure 2. Effect of the average and the variance (CV) of the competitive ranks of the species involved in a triplet on the probability of such triplet to be intransitive. Asterisks indicate significant differences according to the permutation tests performed to control for pseudo-replication when obtaining the *P*-values. Predictors for intransitivity in bacteria were tested one at a time, as only one triplet was intransitive.

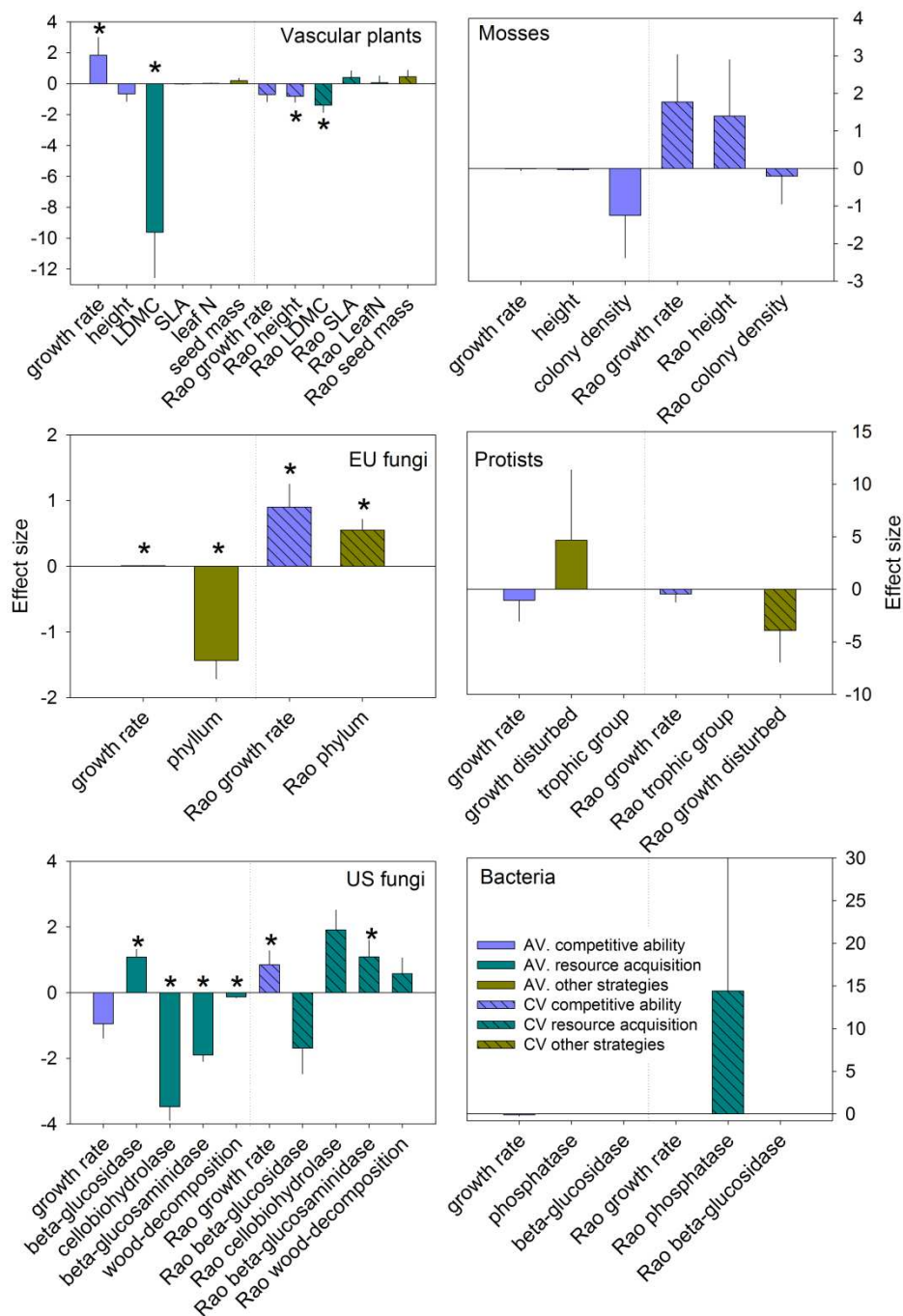


Figure 3. Effect of functional traits related to competitive ability (blue), resource acquisition (green) or other strategies (yellow; response to disturbances, trophic group) on the probability of each three-species combination to be intransitive. The effect (\pm standard error) of both the average (AV) and the variance (calculated as the RaoQ; dashed columns) is shown. Asterisks indicate significant differences according to the permutation tests performed to control for pseudo-replication when obtaining the *P*-values.